Genetic analysis of behavior traits in swine production ☆

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ABSTRACT

Estimates of genetic parameters related to pig behavior under stressful situations are required before selection programs can be designed to produce more docile pigs. Pig behavior was evaluated in a pedigreed Landrace–Duroc–Yorkshire composite population. Piglets were evaluated for their response to handling at 1 d of age ($n=11069$), being placed on their back for 60 s at ~ 24 d of age ($n=975$), and being confined in a scale while backfat measurements were being collected ($n=9035$). Feeding behavior was monitored in a growing–finishing facility ($n=1162$) including preferences for feeding positions. Feeders were placed along a fence with one end adjacent to a gate (gate-end) and the other end open. An animal model was fitted to the data using WOMBAT where litter was included for d 1 activity scores and backtest traits. Fixed effects of sex, pen/year-season/date of collection in all analyses along with scorer (d 1 activity score) and a covariate of age (d 154 weight and backfat). Multiple trait models were fit to estimate genetic covariances among traits. All estimates of heritability were significantly different than zero. Activity scores and backtest traits had the lowest estimates of heritability (0.15–0.19), measures of feeding behavior were more variable (0.16–0.60) while production data had high heritabilities (>0.5). Genomic heritability estimates were similar to standard heritability estimates for most traits, except traits measured at a young age. All traits measured during the backtest had strong genetic correlations and similar estimated heritability. Among feeding behavior traits, number of meals/d and average meal length were highly correlated with total daily meal time. In addition, animals that preferred to eat alone avoided the open-end position at the feeder. The only behavioral traits with genetic correlations significantly different from zero with production traits were associated with feeding behavior where animals that ate longer meals and spent more time at the feeder/d tended to be heavier and fatter at 154 d. In addition, animals that ate more meals/d were fatter and animals that preferred the gate-end position of the feeder were heavier. Pigs with more reactive personalities tended to eat fewer meals/d, each longer in duration, and they preferred the gate-end feeder position. The measures of pig behavior studied were heritable and selection for more docile pigs should not have large detrimental effects on performance.

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1. Introduction

Stress in livestock reduces production, and is a well-being or welfare concern. Stressors can be production environments, interaction with humans or other animals in their pen among many other factors. Aggressive animals can cause injuries to other pigs and decrease performance due to the stress they inflict on pen mates. While an initial feature of animal domestication is selection for docility, most selection after domestication is focused on production. Modern swine production facilities rely heavily on automation reducing the number of positive human–pig interaction events (Rushen et al., 1999). As selection focuses on performance when there is less human interaction, fear of humans may inadvertently increase (Rushen et al., 1999). Furthermore, selection of high lean growth pigs may have produced animals which are less able to cope with environmental stressors (Wellock et al., 2004) or are more aggressive (Cassady, 2007).

Understanding an animal's ability to cope with stressors is important to optimize performance. Solutions to improve docility problems include modifications to the production environment, animal handling as well as genetics. However, few studies have been conducted evaluating pig behavior on large groups of pigs raised in a modern commercial production environment. To understand the genetic architecture of behavior and formulate a genetic solution to animal stress response, estimates of the genetic parameters for behavior traits are needed. Ideally, measurements of behavior should be collected early in life to permit selection.

Genetic influences on coping behavior, activity scores and feeding behavior have each been individually documented. Velie et al. (2009) evaluated multiple measures of pig behavior including coping and aggressive behavior measures. They found that considerable genetic variation existed for behavior traits recorded during the backtest with estimates of heritability being 0.49 for total time spent struggling and 0.53 for number of attempts to escape. Likewise, Turner et al. (2009) estimated heritabilities for multiple measures of aggression in pigs to range between 0.31 and 0.43. Activity scores while collecting weights and backfat measurements were studied by Holl et al. (2010) and Schneider et al. (2011). Both studies found this measure to be heritable (0.23) and genetically correlated with weight at 154 d. Studies have been conducted evaluating the feeding behavior using individual feeding stations and estimated moderate heritabilites for feeding behavior (Chen et al., 2010) and QTL have been identified (Zhang et al., 2009). However, the pigs in these studies are protected/secluded from pen mates while feeding which is not representative of commercial production. Unfortunately, comprehensive studies evaluating multiple pig behavior traits are lacking. While selection can obviously change the behavior of pigs, additional estimates of heritability for behavior traits as well as genetic correlations with performance traits are needed before a selection index can be derived.

Therefore, measures of coping behavior, activity scores and feeding behavior were collected in a pedigreed population managed similar to commercial production systems to estimate components of genetic variation. In addition, this study attempted to determine which, if any, of the behaviors recorded were associated with pig performance, measured as weight and backfat depth at approximately 154 days of age.

2. Materials and methods

2.1. Phenotypic measurements

A composite population of 1/2 Landrace 1/4 Duroc 1/4 Yorkshire described by Holl et al. (2008) was studied. Animals included in the analyses were from generations 5 through 10 after the population was closed. Two distinct, but partially overlapping, experiments were conducted to collect data for estimation of heritability for traits measured during a backtest and measures of feeding behavior. In addition, standard production data collected at USMARC analyzed included activity scores at day 1 and 154, as well as weight and backfat depth at 154 d of age. All measurements recorded were approved by the U.S. Meat Animal Research Center's Animal Care Guidelines and conformed to the Guide for Care and Use of Agricultural Animals in Research and Teaching (FASS, 2010).

2.1.1. Activity scores

In March of 2006, observation of activity during collection of weight and ultrasonic measures of backfat depth at approximately 154 d of age (154AS) was initiated. These measures began on animals born in November of 2005 and continued throughout all farrowing groups produced through the end of 2010. The description of measurements and results of earlier analyses on a subset of the animals included in this study have been reported (Holl et al., 2010; Schneider et al., 2011). Briefly, the scoring system ranged from 1 (animal remained calm with little movement) to 5 (animal vocalizing and attempting to escape). Measurements were recorded on all gilts and boars who were potential candidates for breeding, as well as barrows that were being studied for behavior or carcass evaluation. A total of three people have evaluated pigs at 154 d, but over 90% of the evaluations were conducted by one evaluator. All pigs evaluated on the same day were evaluated by the same person.

Beginning in January 2008 an assessment of activity was made at 1 day of age while caretakers were conducting routine evaluation of the piglet and counting the number of teats (1AS). This is the first time a piglet is routinely handled and secluded from its littermates. A five point scoring system similar to the one developed for 154AS was created. Descriptions of behaviors characterized for scores of 1, 3 and 5 were defined as

1: Animal remained extremely calm during handling.
3: Animal vocalized and attempted to escape during a portion of the handling.
5: Animal constantly vocalized and attempted to escape during handling.

Animals whose behavior was intermediate to these rankings were scored as either a 2 or 4, as appropriate. Five different people evaluated piglets at 1 d of age and more than one person conducted evaluations on most days.

2.1.2. Backtest

Piglets born in the November seasons of 2008 and 2009 as well as piglets born in the July 2008 season were evaluated using a standard backtest as described (Hessing et al., 1993). Piglets were evaluated once 2 d after weaning, at approximately 24 d of age before actual transfer to the nursery. The backtest was performed on 2–6 piglets within a litter selected to represent the complete range of day 1 activity scores within each litter. Approximately equal numbers of gilts and barrows were phenotyped within each litter and use of cross-fostered piglets was avoided. A similar number of piglets were phenotyped for each sire used in that breeding season. Twelve sires were represented in the January 2008 season. A different set of 12 sires produced the next two groups of pigs (July 2008 and January 2009).

Piglets were placed on their backs and the testing began immediately after the animal became calm. The test lasted for 60 s, or until the animal became calm if they were actively struggling at the end of the 60 s test. All animals were evaluated by the same observer for the entire study. Traits analyzed were time until the initial struggle or latency time (LT), number of struggle events (#S) and total time spent struggling (ST).

2.1.3. Feeding behavior

A system was developed to monitor feeding behavior in pigs (Brown-Brandl et al., 2011). A corn–soybean meal balanced mash diet was provided ad libitum. Data were collected on pigs born in July 2008 and January 2009 which also had backtest data recorded. After the conclusion of the backtest study, three additional groups of pigs were fed where feeding behavior data were recorded. Between 240 and 252 pigs began in each replicate and monitoring began when the pigs were moved to the finishing building at eight to ten weeks of age. Monitoring ended when the animals reached market weight (approximately 120 kg body weight) or at approximately 180 d of age when gilts were transferred to the breeding and gestation area for heat detection.

Six pens were filled with 40–42 pigs in each pen, providing ~0.8 m^2/pig and the building was filled five times throughout the study. In three replicates, barrows and gilts were comingled in all six pens. One replicate had five pens of gilts and one pen of barrows, while the final replicate had one pen of barrows and five pens of comingled barrows and gilts. Co-mingled pens had approximately equal numbers of barrows and gilts in each pen. All pigs had an electronic identification ear tag (EID tag) fit at the time of placement in the facility. Pens contained one feeder with five feeding spaces, each equipped with an antenna to detect EID tags within 30 cm. Feed was available ad libitum. Every 20 s each antenna would determine the identification number of the animal with their head in the feeder (or if no pigs were eating) and animal ID, time and antenna number were recorded. A minimum of two consecutive data points were required to constitute a meal. Meal length was calculated as number of consecutive data points times 20 s; thus the minimum length of a meal was 40 s. Average number of meals per day, average daily time spent at the feeder and average length of each meal were computed and analyzed. Approximately 5% of pigs originally penned had incomplete data. Some pigs were removed due to health reasons. Other animals lost their ear tag or the transponder malfunctioned. Only barrows and gilts with at least 21 d on test were included in the analyses.

All data were included for analyses evaluating preferences in feeder position. Feeders were positioned with one end of the feeder approximately 0.5 m from a gate (gate-end). Percentage of meals consumed at the gate-end position of the feeder as well as the percentage of meals consumed at the opposite (open) end was determined for each pig. The percentage of meals consumed when no other pig was at the feeder as well as the mean number of pigs at the feeder during all meals was computed for each pig.

2.1.4. Production data

Standard production procedures at USMARC collect weight and ultrasonic backfat depth on all potential breeding candidates as well as animals on specific growth or carcass studies at approximately 154 d of age. Most backfat measures used an A-mode ultrasound machine (Renco Lean-Meater; Minneapolis, MN); however, a real-time ultrasound machine (ALOKA 500SSD; Wallingford, CT) was used on a subset of animals. A preliminary analysis indicated that both methods to estimate backfat thickness had the same heritability and the genetic correlation between the methods was near unity. However, the mean and variance of the two methods were different. Therefore, backfat thickness data were converted to a standardized value (deviation from the mean value divided by the standard deviation for the method of measurement) and analyzed as a single trait. Analyses only used production data from animals with at least one behavior measurement recorded.

2.1.5. Genotypic data

Genomic DNA from the tails of 2007 animals phenotyped for behavior traits were genotyped using the Illumina PorcineSNP60 BeadChip containing 64,232 single nucleotide polymorphisms (SNP) (Illumina, San Diego, CA; Ramos et al., 2009). Genotypes were scored for 59,895 SNP spanning the entire swine genome. Any SNP with unknown chromosome position, based on build 10.2 (http://www.ncbi.nlm.nih.gov/projects/mapview/map_search.cgi?taxid=9823), those located on SSCY, those with call rates < 95%, or minor allele frequencies < 0.05 were excluded from the data set. Animals were eliminated for call rates < 95% or for failing a Mendelian segregation (parentage) test. After utilizing these quality control measures, a total of 41,848 markers qualified for association analyses.

2.2. Statistical analyses

WOMBAT (Meyer, 2007) was used to estimate components of variation as described (Meyer, 2010). Initially, single trait models were run to identify appropriate models and obtain starting value estimates for variances in multiple trait models.

Initial models for traits recorded while piglets were in the farrowing crates (1AS, LT, #S and ST) included the random effects of animal, birth dam and litter and fixed effects of sex, farrowing group and observer (only for 1AS). Random effects of animal, birth dam and litter were assumed to be distributed $N(\mathbf{0}, \mathbf{A}\sigma^2_{\text{additive}})$, $N(\mathbf{0}, \mathbf{A}\sigma^2_{\text{maternal}})$ and $N(\mathbf{0}, \mathbf{I}\sigma^2_{\text{litter}})$, respectively; where $\mathbf{A}$ was the numerator relationship matrix among animals and $\mathbf{I}$ was the identity matrix. For all analyses, estimates for $\sigma^2_{\text{maternal}}$ was virtually zero so this random effect was removed from final models ran.

Models fit for feeding behavior traits included the random effect of animal and fixed effects of sex and farrowing group/pen. The distribution of the random animal effects was assumed to be $N(\mathbf{0}, \mathbf{A}\sigma^2_{\text{additive}})$, where $\mathbf{A}$ was the numerator relationship matrix among animals. For data collected at 154 d a covariate for age was included to the model fitted for feeding behavior traits. No effect of evaluator for 154 d activity score was included as it was completely confounded with the farrowing group/pen effect.

Multiple trait models fit the same effects as in the final single trait models. Estimates of variance components for random effects from single trait models were used as priors for multiple trait analyses. Comprehensive multiple trait models were ran for the feeding behavior and backtest experiments. Activity scores and production data were analyzed together. Due to convergence issues, not all traits across experiments were analyzed together. To complete the estimation of genetic covariances among all traits, groups of three to five traits were run in multi-trait analyses.

Genomic variance that could be attributed to genetic markers was estimated with a Bayes C model averaging approach (Kizilkaya et al., 2010) using GENSEL (http://bigs.ansci.iastate.edu) as described in Schneider et al. (2012). Single trait analyses were conducted and used genotypic data collected with the Illumina PorcineSNP60 BeadChip (Ramos et al., 2009). Only genotyped animals were included in analyses. Statistical models similar to the WOMBAT analyses were fitted with the exception that litter was considered a fixed effect and no pedigree information was included.

3. Results

Descriptive statistics of the data analyzed in this study are presented in Table 1 and the distribution of animals with multiple types of data in Table 2. Estimates of variance components and heritabilities from single trait models for each trait are reported in Table 3. All estimates of heritability were significantly different ($P < 0.05$) than zero. Variation due to litter effects was approximately 50% greater than the additive genetic variation for d 1 activity score and estimates of litter variance for the backtest traits were similar to the estimates of additive genetic variance. The most significant estimates of heritability were for the production traits, weight and backfat at 154 d of age (0.535 and 0.562, respectively). The estimates of heritability for activity scores and backtest traits were the lowest and ranged between 0.148 and 0.188. The estimates of

heritability for feeding behavior traits ranged from 0.157 (percentage of meals consumed near the gate) to 0.604 (average meal length). Estimates of heritability for feeder position preferences were the lowest (0.157 for gate-side and 0.213 for the open-side) whereas estimates for meal characteristics and number of pigs at the feeder while consuming meals were moderately to highly heritable (between 0.315 and 0.604).

Table 4 presents estimates of heritabilities, genetic and phenotypic correlations from multiple trait models. All measures recorded from the backtest were highly correlated, genetically and phenotypically, as well as had similar heritabilities. Among the feeding behavior traits, number of meals and average meal length were not correlated ($r^2_g = 0.062 \pm 0.162$), but both were significantly correlated with total

Table 1
Descriptive statistics of phenotypic data analyzed.

Trait	Number of records	Mean	Standard deviation
Activity score			
Day 1	11,069	1.82	0.83
Day 154	9035	2.06	1.04
Backtest			
Struggle attempts	975	1.38	1.11
Latency time, seconds	975	27.90	23.21
Struggle time, seconds	975	10.03	9.25
Feeding behavior			
Number of meals/day	1162	13.12	3.99
Average meal length, seconds	1162	320.93	96.63
Daily meal time, minutes	1162	67.87	25.45
Percent meals alone	1162	27.85	7.18
Average number of pigs	1162	2.01	0.14
Percent meals at gate	1162	22.04	9.44
Percent meals in open	1162	20.77	8.91
Production data (154 days)			
Mid-rib backfat (standardized)[a]	9048	0.02	1.20
Weight, kg	9063	93.22	10.56

[a] Mid-rib backfat was standardized based on type of ultrasound machine used. The values for the raw data was a mean of 0.0 and a standard deviation of 1.0.

Table 2
Distribution of animals with multiple traits recorded[a].

Trait	1AS	154AS	Backtest	Feeding	Backfat	Weight
1AS	11,069	4827	975	1162	4841	4855
154AS		9035	774	1120	8725	9035
Backtest			975	489	794	802
Feeding				1162	1138	1148
Backfat					9048	9046
Weight						9063

[a] Trait definitions are: 1AS is day 1 activity score, 154AS is day 154 activity score, Backtest represents all data collected during the backtest, Feeding includes all traits measured with the electronic feed monitoring system, Backfat is mid-loin backfat depth estimated ultrasonically at 154 days of age, and Weight is weight at 154 days of age.

Table 3
Estimates of variation and genetic parameters from single trait analyses.

Trait	Residual variance	Genetic variance	Litter variance	Phenotypic variance	Heritability	Heritability standard error	P-value
D 1 Activity score	0.364	0.090	0.142	0.596	0.151	0.033	3.00E-06
Latency time (s)	378.610	82.265	56.406	517.28	0.159	0.079	0.0223
Number of struggles	0.878	0.192	0.150	1.219	0.157	0.075	0.0184
Struggle time (s)	58.059	12.410	13.286	83.755	0.148	0.076	0.0260
Number of meals	8.70	4.00		12.70	0.315	0.075	1.58E-05
Average meal length (s)	3078.0	4687.6		7765.6	0.604	0.087	6.01E-12
Daily meal time (m)	346.80	203.56		550.36	0.370	0.079	1.82E-06
Percentage of meals alone	14.167	9.108		23.275	0.391	0.076	1.93E-07
Average number of pigs at feeder	0.00403	0.00427		0.00830	0.514	0.081	2.48E-10
Percentage of meals at gate-side	67.550	12.585		80.134	0.157	0.056	0.00263
Percentage of meals at open-side	53.747	14.508		68.256	0.213	0.070	0.00123
D 154 Activity score	0.790	0.183		0.974	0.188	0.025	1.28E-13
D 154 Backfat	0.463	0.594		1.057	0.562	0.028	1.83E-66
D 154 Weight	190.18	218.56		408.74	0.535	0.027	3.19E-65

daily meal time ($r_g^2=0.653\pm0.097$ and 0.678 ± 0.087, respectively). The only genetic correlation significantly different than zero between these three feeding behavior traits and the remaining feeding behavior traits was that for average meal length and number of pigs at the feeder ($r_g^2=-0.312\pm0.124$). Genetic correlations among percentage of meals consumed alone, average number of pigs at the feeder during meals, and percentage of meals consumed at the open position were significantly different than zero, where animals that tended to eat their meals alone had a lower average number of pigs at the feeder and they tended to avoid the open-side of the feeder. The genetic correlation between d 1 and d 154 activity scores was extremely low ($r_g^2=0.104\pm0.137$) and not significantly different than zero.

The only genetic correlations between performance and behavior that were significantly different than zero were with feeding behavior traits (Table 4). Genetic correlations indicated animals that ate longer meals were both heavier and fatter at 154 d of age ($r_g^2=0.356\pm0.101$ and 0.474 ± 0.098, respectively); similar trends were also seen for animals that spent more time eating/day ($r_g^2=0.339\pm0.113$ and 0.593 ± 0.101, respectively). The estimated genetic correlation indicated animals consuming more meals/day were fatter ($r_g^2=0.313\pm0.141$), while animals that preferred to eat at the position nearest the gate were heavier at 154 d of age ($r_g^2=0.573\pm0.142$).

Genetic correlations across different types of behavior measurements revealed the following trends (Table 4). First, pigs with a greater latency period during the backtest ate more meals with shorter average meal lengths ($r_g^2=0.599\pm0.274$ and -0.460 ± 0.225, respectively). Overall, these pigs spent more time at the feeder per day and preferred positions other than the gate-side position ($r_g^2=0.772\pm0.222$ and -0.641 ± 0.273, respectively). To the contrary, pigs that had more struggle attempts or longer struggle times had longer average meal lengths ($r_g^2=0.509\pm0.205$ and 0.451 ± 0.222, respectively). Pigs with greater struggle times spent less time at the feeder each day and preferred to eat at the gate-side position ($r_g^2=0.960\pm0.338$ and 0.741 ± 0.271, respectively), while pigs with more struggle attempts also preferred the gate-side position and ate when fewer pigs were at the feeder ($r_g^2=0.769\pm0.250$ and -0.499 ± 0.240, respectively).

Estimates of genomic additive variance associated with genetic markers are presented in Table 5. Based on these values, genomic selection would be very effective in modifying average length of meals ($h^2=0.696$), backfat ($h^2=0.494$), total meal time per day ($h^2=0.476$), and weight at 154 days of age ($h^2=0.435$). Moderate progress could be made for number of meals per day ($h^2=0.296$). Estimates of genomic heritability were less than 0.10 for feeder position preferences, number of struggles during the backtest and time spent struggling during the backtest.

4. Discussion

An animal's response to a stressor is a complex process that includes physiological, neuroendocrinological, and behavioral modifications (van Erp-van der Kooij et al., 2000). These responses are likely initiated in the brain and mediated through the neuroendocrine system, often inhibiting growth, reproduction, and feeding (Muráni et al., 2010). Therefore, minimizing the incidence or frequency of stressful events will improve animal performance. A majority of research efforts have focused on modifications or pre-exposure to environmental factors to minimize stress, but selection offers additional opportunities to reduce stress in livestock (Newman, 1994). Modifying an animal's ability to cope with stress (coping style) by selection is possible (Velie et al., 2009), and would potentially result in pigs that are less aggressive towards caretakers and other pen mates.

The primary measure to evaluate coping style in the current study was the backtest. Velie et al. (2009) evaluated pigs using this technique and estimated higher heritabilities for number of struggles and total struggle

Table 4
Mutli-trait genetic and phenotypic parameter estimates[a,b,c].

Trait	1AS	LT	#S	ST	#Meals	AveMealT	DMealT	Alone	Groupsize	Gate	Open	154AS	BF	WT
1AS	0.151	−0.386	0.047	0.104	0.209	0.123	0.306†	−0.366*	0.428*	−0.276	0.264	0.104	−0.046	0.087
LT	−0.046	0.142	−0.914***	−0.922***	0.599*	−0.460*	0.772***	−0.068	0.535†	−0.641*	−0.070	0.097	−0.215	−0.243
#S	0.059	−0.765***	0.155	0.802***	−0.375	0.509*	−0.080	0.306	−0.499*	0.769**	−0.170	0.020	0.146	0.249
ST	0.051	−0.703***	0.799***	0.154	−0.331	0.451*	−0.960**	0.031	−0.171	0.741**	0.069	0.274	0.070	0.216
#Meals	0.051†	0.139*	−0.068	−0.043	0.312	−0.062	0.653***	−0.274†	0.134	−0.097	0.004	−0.043	0.313*	0.049
AveMealT	0.023	−0.113*	0.163***	0.107*	0.006	0.606	0.678***	0.213	−0.312*	0.026	−0.115	−0.073	0.474***	0.356***
DMealT	0.053†	0.068	0.059	0.040	0.739***	0.618***	0.411	−0.028	−0.144	0.004	−0.057	−0.111	0.593***	0.339**
Alone	−0.031	−0.012	0.035	0.006	−0.047	0.197***	0.075*	0.409	−0.937***	0.179	−0.425*	0.036	0.193	−0.059
GroupSize	0.042	−0.005	−0.083	−0.029	0.020	−0.256***	−0.136***	−0.958***	0.529	−0.263	0.339*	−0.073	−0.137	0.008
Gate	−0.015	−0.130**	0.110*	0.097*	0.032	0.072*	0.080*	−0.013	0.003	0.176	0.084	−0.118	0.139	0.573***
Open	−0.005	0.035	−0.012	0.022	−0.004	−0.060	−0.042	−0.075*	0.041	−0.398***	0.244	−0.149	0.246	0.038
154AS	0.029†	0.066†	−0.032	0.035	0.046	0.001	0.031	−0.005	−0.001	−0.036	−0.001	0.190	−0.106	−0.112
BF	0.002	−0.046	0.032	0.015	0.149***	0.227***	0.280***	−0.089*	0.067†	0.092*	0.106**	−0.023	0.562	0.415***
WT	0.020	−0.074	0.071	0.075†	0.032	0.162***	0.141***	−0.186***	0.122**	0.186***	0.074*	−0.048**	0.449***	0.534

[a] Genetic correlations are presented above the diagonal, phenotypic correlations are below the diagonal and heritabilities are on the diagonal. Traits were analyzed in sets 3 to 5. Heritabilities were averaged across analyses and subtle differences with the heritabilities obtained with single traits analyses will be noticed (Table 3); thus no indication of level of significance is provided.

[b] Trait definitions are: 1AS is the day 1 activity score, LT is the latency time until first struggle in the backtest, #S is the number of struggle attempts during the backtest, ST is time spent struggling during the backtest, #Meals is the average number of meals/day, AveMealT is the average length of a meal, DMealT is the total time at the feeder during an average day, Alone is the percentage of time spent at the feeder when no other pigs were eating, Groupsize is the average number of pigs at the feeder when the pig was feeding, Gate is the percentage of time the pig occupied the end position near the gate, Open is the percentage of time the pig occupied the end position on the open end of the feeder, 154AS is day 154 activity score, BF is backfat depth at 154 days of age, and WT is weight at 154 days of age.

[c] Estimates that were significantly different from zero are indicated by their level of significance. † $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 5
Estimates of genomic variance associated with Illumina PorcineSNP60 markers based on GENSEL analyses.

Trait	Number of pigs	[a]Genomic h^2	Variances		
			Genetic	Residual	Phenotypic
D 1 Activity score	878	0.0384126	0.022319	0.558703	0.581022
Latency time	740	0.115127	51.4276	395.275	446.7026
Number of struggles	740	0.0173088	0.017922	1.01753	1.035452
Struggle time	740	0.0612939	4.23603	64.8741	69.11013
Number of meals	486	0.295961	1.68723	4.01362	5.70085
Average meal length	486	0.696311	5779.23	2520.56	8299.79
Daily meal time	486	0.476188	121.391	133.531	254.922
Percentage of meals alone	486	0.0897517	1.6496	16.7299	18.3795
Average number of pigs at feeder	486	0.149389	0.000979	0.005576	0.006555
Percentage of meals at gate-side	486	0.0976705	7.72614	71.378	79.10414
Percentage of meals at open-side	486	0.0334908	2.36506	68.2531	70.61816
D 154 Activity score	1988	0.119399	0.093112	0.686729	0.779841
D 154 Backfat	2007	0.493748	0.668216	0.685139	1.353355
D 154 Weight	1988	0.435209	130.445	169.284	299.729

[a] Genomic h^2 = proportion of phenotypic variance explained by additive effects of genetic markers. This is an estimate of heritability in the narrow-sense.

time (0.54 and 0.49, respectively) than the estimates in the current study (0.155 and 0.154, respectively). However, Velie et al. (2009) measured each piglet twice and analyzed the combined data which reduces environmental/error variance resulting in higher heritabilities. Velie et al. (2009) also estimated heritabilities for single measures of total time spent struggling and the results were closer to the current study's estimate (0.38 and 0.40). In addition, Velie et al. (2009) performed the backtest at an earlier age (7 and 14 d vs ~24 d). Our decision to wait until after the piglets were weaned was to eliminate effects due to the sow's reaction to the backtest as all tests were conducted in the farrowing room; however, this decision may have increased variation that was not parameterized resulting in lower estimates of heritability. Velie et al. (2009) found that the number of struggle attempts was positively correlated (phenotypic) with weight adjusted backfat, whereas van Erp-van der Kooij et al. (2000) estimated a negative phenotypic correlation between number of struggle attempts and weight adjusted backfat. Spake et al. (2012) did not find any association of backtest results with resident-intruder or novel-object tests implying that the backtest was not predictive of aggression or exploratory behaviors later in life. In our study, neither the phenotypic nor the genetic correlations were significantly different than zero between any of the backtest measurements and backfat at 154 days of age (unadjusted for weight) but the trend was for less responsive animals to be leaner which corresponds with the results of Cassady (2007).

Another measure of coping style is how the animal reacts when confined with close human contact. We previously have shown that an animal's response to seclusion in an enclosed scale while backfat depth is estimated ultrasonically is moderately heritable (Holl et al., 2010). The activity scoring system developed by Holl et al. (2010) was expanded by including an assessment at 1 day of age. This is the first time a piglet is picked up and held by a caretaker and is secluded from its littermates; thus representing several novel stimuli to the piglet. The *a priori* hypothesis was that an assessment at 1 day of age would provide similar information as the day 154 assessment. Unfortunately that was not the case as these two traits were neither phenotypically ($r_p^2 = 0.029 \pm 0.016$) nor genetically ($r_g^2 = 0.104 \pm 0.137$) correlated. The only behavior trait that day 1 activity score was associated with was the average number of pigs at the feeder when the pig was feeding ($r_g^2 = 0.428 \pm 0.159$). Therefore, despite the early measurement and ease of data collection, day 1 activity scores appear to have limited utility for future selection criteria in pigs.

The estimated genetic correlations between day 154 activity score and production traits ($r_g^2 = -0.112 \pm 0.074$ and -0.106 ± 0.073 for weight and backfat, respectively), though not significantly different than zero, were similar to the estimates of Holl et al. (2010) where animals with greater activity scores tended to be lighter and leaner. Similar phenotypic correlations were observed by Yoder et al. (2011). Parallel trends have been reported in beef cattle where flight speed is negatively correlated with weaning weight and average daily gain (Müller and von Keyserlingk, 2006; Sant'Anna et al., 2012). Furthermore, cattle that remain calm when restrained in chutes have greater average daily gain (Turner et al., 2011). These studies indicate that animals which are more excitable when secluded in close proximity to humans may be allocating fewer resources to growth during the finishing phase. The magnitude of all genetic correlation estimates between day 154 activity score and feeding behavior in the current study were quite small and not significant indicating that active animals were at the feeder for a similar amount of time as calm animals. The estimated genetic correlation between struggle time and d 154 activity score was positive ($r_g^2 = 0.274$) and approached significance ($P = 0.133$), reflecting that animals with a more reactive coping style were detected with both measurements. While backtest data are available earlier in a pig's life, collection of backtest data is more time-consuming than

scale activity scores. Therefore, neither trait may be an ideal fit for commercial application.

Numerous reports on feeding behavior have been published. Most studies have used a single, electronically monitored, individual feeding station per pen where the animal is either completely or partially protected from pen mates while eating. A small set of studies have used video recording to observe feeding behavior (for a short period of time) with multi-position feeders. Commercial systems use multi-position feeders where pigs need to adjust to the social interactions of their penmates. The current study is the only study where behavior was electronically monitored during the entire finishing phase using a 5-position feeder that provided no protection from other pigs. Thus, the feeding behavior traits recorded in the current study are quite novel and may be different than those reported using other feeding systems. The average number of meals per day in the current study (13.1) was considerably greater than the reported values of Lewis and McGlone (2008) of 5.6, Young et al. (2011) of approximately 6.5, Houston et al. (2005) of 6.7, Rauw et al. (2006) of 7.5, and Zhang et al. (2009) of 8.9. However, the values reported by de Haer et al. (1993) of 11.7, Estany et al. (2002) of 13.1 and Hyun and Ellis (2002) of 11.8 were similar to the present study. Georgsson and Svendsen (2002) had much higher average number of visits per day ranging from 25 to 50 with a single position system that only provided partial protection from pen mates, similar to the feeders used by de Haer et al. (1993). In a study evaluating both types of feeders, Nielsen et al. (1996) showed that pigs in pens with multiple position, unprotected feeders had considerably more meals than pigs in pens with a single space, completely enclosed feeder (53.5 versus 9.2, respectively).

The average meal length (320 s) was shorter in the present study than that reported by Houston et al. (2005), Hyun and Ellis (2002), Lewis and McGlone (2008) and Young et al. (2011), but longer than Georgsson and Svendsen (2002) reflecting the observation that when pigs increase the number of meals per day, the length of each meal tends to be shorter (Lewis and McGlone, 2008). Nielsen et al. (1996) compared feeder visits between individual feeding stations and a 4-position feeder in pens of 10 boars and found that pigs in the individual feeder systems had fewer meals but more total time eating (ie. meals of much longer duration); however, their design did not normalize the number of pigs/feeding position and so there may be a confounding of feeder type and pig density. The total time spent feeding per day (68 min) was similar to most studies (Estany et al., 2002; Georgsson and Svendsen, 2002; Rauw et al., 2006), but slightly more than the times reported by Chen et al. (2010) of 47 min, Nielsen et al. (1996) of 49 and 59 min, Houston et al. (2005) of 56.6 min, and de Haer et al. (1993) of 56.9 min.

Numerous factors have been shown to alter feeding behavior. The most studied factor is number of pigs per feeding position. As the density of pigs per position increases, pigs typically will have fewer meals, each of longer duration (Georgsson and Svendsen, 2002; Hyun and Ellis, 2002). However, at the stocking densities studied (2–12 pigs per feeder position), stocking density did not

affect performance or result in increased aggressive behavior in any study. While environmental factors affect many behavior traits in pigs, Nakamura et al. (2011) did not observe differences in feeding behavior among pigs confined in an indoor facility versus pigs reared in an outdoor pen. However, Choi et al. (2011) did observe that temperature and relative humidity significantly affected feeding behavior. The type of feed provided could also alter feeding behavior. For all studies reviewed as well as the current study, a dry feed was provided ad libitum. However, the feed provided in the current study was a mash, where as in most other studies it was either a pellet or a crumble. Research on how feed type affects feeding behavior should be studied further.

Most genetic studies that have collected individual feeding data have focused on feed efficiency, rather than feeding behavior traits. Nonetheless, feeding behavior traits have been found to be heritable as indicated by estimated heritability and association with genetic markers. Chen et al. (2010) estimated heritability for daily feeding time to be 0.38, very similar to our estimate of 0.37 in the current study while de Haer and de Vries (1993) estimated the heritability to be 0.24. de Haer and de Vries reported a higher heritability estimate (0.45) for number of meals per day than the present study (0.31) but a lower heritability estimate for average meal time (0.27 versus 0.60). Houston et al. (2005) discovered a QTL for daily feeding time located on chromosome 6 that may be responsible for a portion of the reported heritability. Zhang et al. (2009) detected 2 QTL for number of meals per day located on chromosomes 7 and 9. Our analysis of genomic heritability (phenotypic variation associated with genetic markers) implies that the current dataset could identify QTL and/or be used to apply genomic selection on both traits. Applying genome-wide association analyses to the current data set may support previous studies and/or identify novel genomic positions that affect feeding behavior.

Some animals preferred to consume meals near the gate whereas others preferred to consume meals at the open end position of the feeder. While the position near the gate could be perceived as a 'safe' place where aggressive animals may only attack from one side, another perception could be that it is a more enclosed location without an escape route. The only significant genetic correlations with percentage of meals consumed on the gate-side indicated that animals preferring this position had shorter latency times ($r_g^2 = -0.641 \pm 0.273$), greater number of struggles ($r_g^2 = 0.769 \pm 0.250$), more total struggle time ($r_g^2 = 0.741 \pm 0.271$) as well as were heavier at 154 d of age ($r_g^2 = 0.573 \pm 0.142$). Animals that preferred the open-side of the feeder consumed fewer meals alone ($r_g^2 = -0.425 \pm 0.165$) and ate when more pigs were at the feeder ($r_g^2 = 0.339 \pm 0.163$). Percentage of meals consumed alone is another trait that could be perceived in two different ways. Did these animals prefer to eat alone or did other animals avoid eating when the animal was at the feeder? Video image recording may help to elucidate the reason that these pigs ate alone. Nielsen et al. (1996) noted that pigs preferentially selected an end position if no other pig was at the feeder. However, they found that if a pig was at the feeder, then the incoming pig more often selected

the feeder position adjacent to the other pig. This reflects the social nature of the pig while feeding and may explain differences observed with other studies where the pig was completely secluded during feeding or when only a single position is available per pen. Nielsen et al. (1996) also observed that pigs often would sample feed from more than one feeder position during a meal. We also observed that more than one feeder position was often used during a meal, but no attempt was made to evaluate this behavior.

The primary conclusion that can be drawn from the current study is that animals which had a more reactive coping style, as evidenced by the backtest or d 154 activity score, tended to have fewer meals per day, but ate for longer periods of time at each meal. They typically preferred to eat when fewer pigs were at the feeder and consumed a greater percentage of their meals at the gate-side feeder position. Therefore, these animals may be more content if more feeders, with fewer feeding positions per feeder, were located around the pen or in smaller pens with fewer pigs. Pigs with less reactive coping styles may be more amenable to large pens and feeders with multiple feeding positions. A consistent trend with production data and coping style could not be seen.

As swine production continues to become more intensified and pigs are selected to grow faster and leaner, there are greater challenges applied to the biological system of the pig. Under these constraints, some pigs may be genetically prone towards aggressive behaviors while others may be too passive and become repeated victims of the aggression (Wilson et al., 2012). Selection for pigs that are less reactive to stressful situations is one approach that could reduce production losses. For selection to be applied in the commercial sector, these data need to be reliable and cost-effective to collect. While the backtest is a standard measure of coping style, this procedure is very labor intensive and does not correlate well with production traits. The d 154 activity score is likely the most economical data to collect and has consistent associations with performance, but is not measured until later in life. We have evaluated activity scores at 98 d of age on a small subset of pigs and those data appeared to be similar to data collected at 154 d of age (data not shown). An assessment at 98 d would be more feasible for commercial production so that selection decisions can be made earlier and might avoid possible effects associated with puberty in gilts. With economical feed monitoring, it may be possible to categorize pigs for specific feeding behaviors typical of pigs with a less reactive coping style (more frequent meals of shorter length, combined with eating in larger groups and no feeder position preference). With these measurements, it should be possible to select for pigs that are less reactive to stressful situations. Another option would be to implement selection through the use of genetic markers. While our estimates of genomic narrow-sense heritability indicated that genomic selection would be quite effective for production and feeding behavior traits, traits associated with reactive or aggressive personalities had very low estimates of genomic heritability.

In conclusion, the behavior traits studied had low to moderate heritabilities and genetic correlations with production traits were either favorable or not significantly different than zero. Selection could be applied to modify the behavior of pigs without large detrimental effects on performance; however, numerous generations will be required to make substantial changes in phenotype for the lowly heritable traits (such as the backtest traits). Implementation of a selection index including Number of meals, Number of pigs at the feeder when eating and day 154 activity score could result in pigs with a noticeably less reactive coping style within a few generations without compromising growth or leanness.

Conflict of interest statement

There are no known conflicts of interest associated with this publication.

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